BIULETYN OCENY ODMIAN
Zeszyt 21 - 22 1989

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GENETIC AND ENVIRONMENTAL VARIABILITY OF YIELDS IN THE OFFICIAL FRG VARIETY PERFORMANCE TESTS

Summary: The magnitude of genetic and environmental variance components was estimated in the official FRG trial system. For 16 crops, over a range of 7 to 11 years, variance components were calculated by the restricted maximum likelihood method (REML). The plot error was the largest component. Varieties × centres and varieties × years components are about the same size, whereas the varieties × centres × years component was 2 to 4 times as large. The varieties component was, in most crops, smaller than the varieties × centres × years component. As the variability depended on the mean yield level of a crop, coefficients of variation were calculated in addition. Open-pollinating winter rye showed less variability than self-pollinating winter cereals. Spring cereals varied less than winter cereals with regard to variance components. Both large variety variance and large interaction variances were found in forage maize, legumes, and potatoes. Small interaction variances were detected in sugar beet. Consequences for the optimal allocation of test capacity and for the estimation of variety performance were discussed.

1. INTRODUCTION

The evaluation of new varieties in the official performance trials is organized in 3-year trial series with up to 30 centres in the third year. Yield, quality, disease resistances, earliness and other important performance characters are evaluated. The best varieties are selected and released for commercial production.

In 1984, the testing system for cereals was changed into an integrated form, with breeder's trials in the first year, official trials, in the strict sense, in the second year, and trials combined with regional variety trials of the federal states in the third year. Components of variance must be known if such trials are to be optimally allocated and analyzed more efficiently, e.g. by best linear unbiased prediction (BLUP). Thus, components of variance are often estimated for a single crop and certain plant material (see the corresponding tables in Talbot 1984 or Utz 1977). However estimation errors were high and appropriate comparisons between crops were seldom possible.

The present investigation was undertaken to estimate components of variance for the most important field crops. Yield data from the previous trial system for cereals were used from 1976-1983 and to 1986 for other crops. Coefficients of variation and heritabilities were calculated to compare variability across crops.

2. MATERIALS AND METHODS

Yield data from the official FRG trials of 16 crops were used in the investigation: winte wheat, winter barley winter rye, spring wheat, spring barley, spring oats, grain and forag maize in two maturity groups each, seed rape, forage pea, field bean, sugar beet, fodde beet, potato in two maturity groups, perennial ryegrass, and cocksfoot.

The trials were established in complete randomized block designs with four replications. Plot sizes were about 10 m^2. Apart from oats, in cereal crops additional nitrogen dressing, as well as fungicides or other agrochemicals, were applied with three levels and arranged in a split plot manner. In herbage trials, the total dry-matter yield per year was considered.

Table 1

Yield data used in analysis

Crop	Years	Average per period			Yield trait	Mean (dt/ha)
		Var.	Cent.	Trials		
Winter wheat	8 (1976 - 83)	31	16	35	grain	68.0
Winter barley	8 (1976 - 83)	26	15	33	grain	65.4
Winter rye	9 (1976 - 84)	11	14	34	grain	55.7
Spring wheat	8 (1976 - 83)	30	14	34	grain	58.6
Spring barley	8 (1976 - 83)	28	17	34	grain	50.7
Spring oats	8 (1976 - 83)	38	15	32	grain	55.2
Grain maize E*	11 (1976 - 86)	17	14	27	grain	83.0
Grain maize L#	11 (1976 - 86)	10	11	25	grain	83.9
Forage maize E	11 (1976 - 86)	26	13	25	TDM §	163.4
Forage maize L	11 (1976 - 86)	13	13	26	TDM	165.2
Seed rape	11 (1976 - 86)	23	12	30	grain	32.7
Forage pea	11 (1976 - 86)	14	9	22	grain	30.9
Field bean	11 (1976 - 86)	8	11	28	grain	42.1
Sugar beet	11 (1976 - 86)	41	14	32	sugar	105.4
Fodder beet	11 (1976 - 86)	15	11	28	DM ‡	151.3
Potato E	11 (1976 - 86)	26	14	28	tuber	446.4
Potato L	11 (1976 - 86)	14	13	28	tuber	444.5
Per. ryegrass	9 (1975 - 83)$	20	8	23	TDM	117.6
Cocksfoot	7 (1977 - 83)$	7	8	20	TDM	134.8

* E=Early
\# L=Late
§ TDM=Total dry matter yield
‡ DM=Dry matter yield
$ Seeding year

The data sets were non-orthogonal, because new varieties were tested for 3 years at most and, after each year, varieties are eliminated. Yet in any particular year, the same set of varieties was tested at each of the centres used in that year. But the data of different trial periods were disconnected with respect to varieties. Therefore, the data matrix was subdivided into overlapping 3-year periods to be analyzed (see table 2 for winter wheat as an example). Only varieties which were tested for two or more years were included. Table 1 shows the extent of the data, in particular the average number of varieties, centres (or locations), and trials per period.

All effects were considered to be random, with the assumption that varieties, centres, and years were random samples of certain populations. The following components were estimated: centres σ^2_c, years σ^2_y, centres × years σ^2_{cy}, varieties σ^2_v, varieties × centres σ^2_{vc}, varieties × years σ^2_{vy}, varieties × centres × years σ^2_{vcy}, and plot error σ^2_e.

The analysis was conducted via the restricted maximum likelihood method (REML) with the aid of a computer program of **Robinson** (1987). REML is an efficient method for analysis of data with a high degree of non-orthogonality (see also **Moro** et al. 1988). The likelihood equations were solved by an iterative technique similar to Fisher's scoring technique. Further details of the method can be found in **Patterson** and **Thompson** (1971, 1975) and comparisons with other methods are made by **Searle** (1988). REML has considerable ability to control bias due to selection (**Rothschild** et al., 1979), which is important for the present data matrix.

To compare the precision of series of trials across crops, heritabilities were estimated as the ratio of genotypic to phenotypic variance by using the estimated components of variance in the equation

$$h^2 = \frac{\sigma^2_v}{\sigma^2_v + \sigma^2_{vc}(C + \sigma^2_{vy})\,Y + \sigma^2_{vcy}((CY) + \sigma^2_e)(RCY)} \tag{1}$$

where C represents the number of centres in a balanced series of trials, Y the number of years, and R the number of replications per trial.

3. ESTIMATES OF VARIANCE COMPONENTS

For each 3-year period, a REML analysis was conducted and the estimated components of variance were averaged. The estimates for winter wheat are given as an example in table 2. From period to period the average performance shows an upward trend. The components contributing most to the phenotypic variance are centres variance $\hat{\sigma}^2_c$, years variance $\hat{\sigma}^2_y$, and centres × years variance $\hat{\sigma}^2_{yc}$. The great range in $\hat{\sigma}^2_y$ and $\hat{\sigma}^2_{yc}$ estimates

Table 2

Estimated components of variance for yield in winter wheat

Period	Mean	Estimated components of variance (dt/ha)²							
		$\hat{\sigma}^2_c$	$\hat{\sigma}^2_y$	$\hat{\sigma}^2_{cy}$	$\hat{\sigma}^2_v$	$\hat{\sigma}^2_{vc}$	$\hat{\sigma}^2_{vy}$	$\hat{\sigma}^2_{vcy}$	$\hat{\sigma}^2_e$
1976 - 78	59.8	10.4	0.0	108.5	12.1	4.8	2.8	12.7	21.7
1977 - 79	63.6	46.1	33.4	58.6	8.8	1.8	3.9	13.0	18.4
1978 - 80	69.6	21.7	0.8	30.9	11.5	0.0	1.3	10.7	13.1
1979 - 81	70.1	31.6	0.0	60.9	7.1	1.4	2.6	11.5	13.3
1980 - 82	71.8	23.9	0.0	113.5	8.2	3.1	1.0	12.8	13.6
1981 - 83	73.1	14.8	0.1	137.9	7.5	2.0	8.6	16.1	18.6
Mean	68.0	24.8	5.7	85.1	9.2	2.2	3.4	12.8	16.4
SE (REML)		26.7	20.6	28.4	3.0	0.9	1.0	– 1.2	–
SE (obs.)	5.2	12.8	13.6	40.9	2.1	1.6	2.8	1.8	3.6
		Standard error for averaged components of variance							
SE (obs.)	2.1	5.2	5.5	16.7	0.9	0.7	1.1	0.8	1.5

is due to the small number of years per period. However these three components are of minor interest, because they do not enter into the calculation of phenotypic variance between variety means nor their standard error.

Table 3

Estimated components of variance for yield

Crop	Components of variance (dt/ha)^2				
	$\hat{\sigma}^2_v$	$\hat{\sigma}^2_{vc}$	$\hat{\sigma}^2_{vy}$	$\hat{\sigma}^2_{vcy}$	$\hat{\sigma}^2_e$
Winter wheat	9.2	2.2	3.4	12.8	16.4
Winter barley	9.4	2.4	2.8	12.1	22.1
Winter rye	4.4	0.9	1.8	4.3	13.5
Spring wheat	2.8	2.7	3.1	8.3	11.9
Spring barley	4.6	1.8	1.2	6.4	13.4
Spring oats	5.1	1.4	0.9	6.0	11.7
Grain maize E*	10.8	2.5	3.5	12.6	24.4
Grain maize L#	12.3	4.4	4.9	13.9	23.1
Forage maize E	82.0	9.6	10.7	58.9	114.2
Forage maize L	71.5	20.0	16.5	53.9	96.2
Seed rape	7.9	0.8	1.2	5.1	9.7
Forage pea	31.5	2.2	3.1	12.1	13.8
Field bean	15.6	5.4	6.8	12.5	14.2
Sugar beet	16.0	1.8	2.5	2.6	42.2
Fodder beet	51.7	11.8	2.3	29.8	115.0
Potato E	1402.	453.	424.	1133.	746.5
Potato L	1355.	333.	816.	869.	1082.
Per. ryegrass	19.7	11.8	2.8	60.0	54.6
Cocksfoot	38.9	14.2	5.4	25.8	47.9

* E=Early
# L=Late

The well-known considerable estimation error of variance components is demonstrated in the last lines of table 2. For some components the standard error is larger than the estimate itself if a single period is considered. The standard error of an estimate averaged over the six periods in winter wheat may be of an acceptable magnitude.

Table 3 shows, in general, that the largest component is the plot error $\hat{\sigma}^2_e$ with the exception of forage pea, field bean, and potato, where the genetic variance $\hat{\sigma}^2_v$ is the largest component. Of the interaction components, varieties × centres $\hat{\sigma}^2_{vc}$ and varieties × years $\hat{\sigma}^2_{vc}$ have similar values, the latter being somewhat larger. These two variances are small than the varieties × years × centres component $\hat{\sigma}^2_{vcy}$. The genetic component, the varieties variance $\hat{\sigma}^2_v$, is close to the varieties × centres × years variance in magnitude.

In detail, winter wheat and winter barley appear to have a larger genetic variance $\hat{\sigma}^2_v$ and larger masking variances $\hat{\sigma}^2_{vc}$, $\hat{\sigma}^2_{vy}$, $\hat{\sigma}^2_{vcy}$, and $\hat{\sigma}^2_e$ than spring wheat and spring barley (Figure 1). The cross-pollinating winter rye has smaller values in all components than the self-pollinating winter cereals (Figure 2). In spring oats the varieties × years variance is lower than in the other two spring cereals.

Grain and forage maize show larger variability components than the small grain cereals, as do sugar and fodder beets and potato. Seed rape, forage pea, and field bean behave intermediately.

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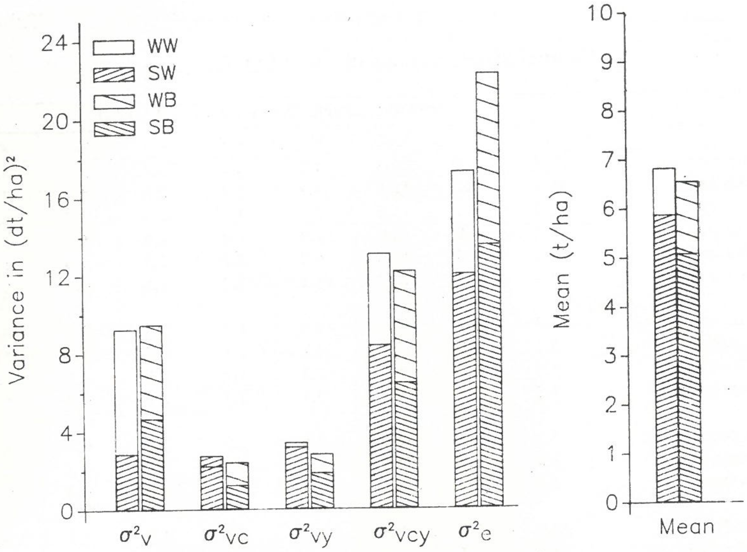

Fig. 1. Components of variance for yield in wheat and barley (WW=Winter Wheat, SW=Spring Wheat, WB=Winter Barley, SB=Spring Barley)

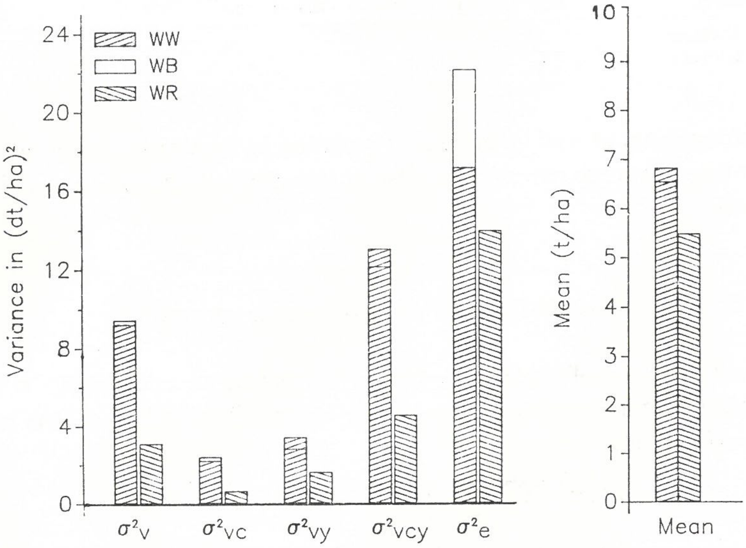

Fig. 2. Components of variance for yield in winter cereals (WW=Winter Wheat, WB=Winter Barley, WR=Winter Rye)

The size of the components of variance is related to the mean performance, which can be pointed out in a comparison of tables 1 and 3. To adjust for this dependency, the coefficients of variation are given in table 4 for each component. The genetic and interaction variation coefficients of winter rye remain lower than those of the other two winter cereals. A larger genetic variation coefficient is found in both groups of forage maize. The greater

Table 4

Estimated coefficients of variation for yield

Crop	Coefficients of variation of component (in %)							
	c_c	c_y	c_{cy}	c_v	c_{vc}	c_{vy}	c_{vcy}	c_e
Winter wheat	7.3	3.5	13.6	4.5	2.2	2.7	5.3	6.0
Winter barley	11.5	7.3	12.1	4.7	2.4	2.6	5.3	7.2
Winter rye	10.2	2.6	13.0	3.8	1.7	2.4	3.7	6.7
Spring wheat	12.3	10.0	12.6	2.9	2.8	3.0	4.9	5.9
Spring barley	11.5	1.4	11.6	4.2	2.7	2.2	5.0	7.2
Spring oats	4.1	8.2	16.0	4.1	2.2	1.8	4.4	6.2
Grain maize E*	8.3	10.3	12.2	4.0	1.9	2.3	4.3	6.0
Grain maize L#	5.8	9.8	13.5	4.2	2.5	2.7	4.4	5.7
Forage maize E	8.0	8.5	9.7	5.5	1.9	2.0	4.7	6.5
Forage maize L	9.2	10.2	10.7	5.1	2.7	2.5	4.4	5.9
Seed rape	7.7	5.2	15.3	8.6	2.7	3.3	6.9	9.5
Forage pea	9.2	9.3	25.8	18.2	4.8	5.7	11.2	12.0
Field bean	3.4	10.6	25.5	9.4	5.5	6.2	8.4	9.0
Sugar beet	12.0	7.0	9.8	3.8	1.3	1.5	1.5	6.2
Fodder beet	11.4	6.5	12.4	4.8	2.3	1.0	3.6	7.1
Potato E	11.9	8.9	16.0	8.4	4.8	4.6	7.5	6.1
Potato L	12.1	8.4	16.2	8.3	4.1	6.4	66.6	7.4
Per. ryegrass	11.2	16.8	13.3	3.8	2.9	1.4	6.6	6.3
Cocksfoot	11.4	13.1	13.0	4.6	2.8	1.7	3.8	5.1

* E=Early
\# L=Late

coefficients of masking, as well as of genetic variation in seed rape, forage pea, field bean, and both potato groups are remarkable. Also noteworthy are the low interaction variances of sugar beets.

4. PRECISION IN BALANCED SERIES

To prove effectiveness of a testing system, it is sufficient to consider the relative magnitude of the variance components. In the average of the six cereal crops, the ratio of components of variance is

$$\hat{\sigma}_v^2 : \hat{\sigma}_{vc}^2 : \hat{\sigma}_{vy}^2 : \hat{\sigma}_{vcy}^2 : \hat{\sigma}_e^2 = 1 : 0.3 : 0.4 : 1.4 : 2.5 \tag{2}$$

Thus the masking variances are, in total, about five times larger than the genetic variance and the three interaction variances are in total as large as the plot error. In maize, legumes, beets, and potatoes, the masking components are smaller, which leads to higher heritability estimates in these crops (table 5).

The heritability can be defined as the proportion of the observed phenotypic variance for which genetic differences are responsible and it is used as a parameter for the precision of the performance trials. Heritability h^2 is a measure ($0 \leqslant h^2 \leqslant 1$) for the carry over of the observed variety differences which can be reproduced in a future trial. The heritability for a test with the minimum of one plot per variety is given in the first column of table 5. The heritability for one plot is mostly very low with the exception of forage pea. Such low heritabilities may be adequate only in the first stages of the breeding process, but not in variety performance testing. Thus it is necessary to increase the heritability by testing with more replications, centres, and years.

Table 5

Estimated heritabilities

Crop	Heritability for	
	S§	M⧧
Winter wheat	0.21	0.84
Winter barley	0.19	0.86
Winter rye	0.18	0.84
Spring wheat	0.10	0.64
Spring barley	0.17	0.85
Spring oats	0.20	0.89
Grain maize E*	0.20	0.85
Grain maize L#	0.21	0.83
Forage maize E	0.30	0.93
Forage maize L	0.28	0.89
Seed rape	0.32	0.93
Forage pea	0.50	0.95
Field bean	0.29	0.83
Sugar beet	0.25	0.93
Fodder beet	0.25	0.94
Potato E	0.34	0.87
Potato L	0.30	0.80
Per. ryegrass	0.13	0.84
Cocksfoot	0.29	0.91
Mean	0.25	0.86

* E=Early
\# L=Late
§ heritability for a single plot (1 year, 1 centre, 1 replication)
⧧ heritability for multiple plots (3 years, 12 centres, 6 replications)

In figure 3 heritability is given as a function of the number of replications, centres, and years, respectively. Each curve is calculated using formula (1) with the underlying variability ratio (2) whereby only one parameter is increased, e.g. number of centres, and the others are held constant to one.

Some important points for variety testing can be discerned from figure 3:

1. The curves increase steeply only for lower numbers of replications, centres or years. For higher values the curves flatten nearly reaching a plateau. Thus little increase in precision is gained beyond two or three replications, or six to seven centres or years. On the other side it is advisible to choose such a number of replications, centres, and years that the steeper ascent of the curves is utilized in testing.

2. Increasing the number of replications is not as advantageous as increasing the number of centres or years. The level and increment in heritability are always higher for increasing numbers of centres or years than for increasing numbers of replications. A test with, say 1000 replications in one year and one centre, is only as precise as a test with one replication in one year and two centres.

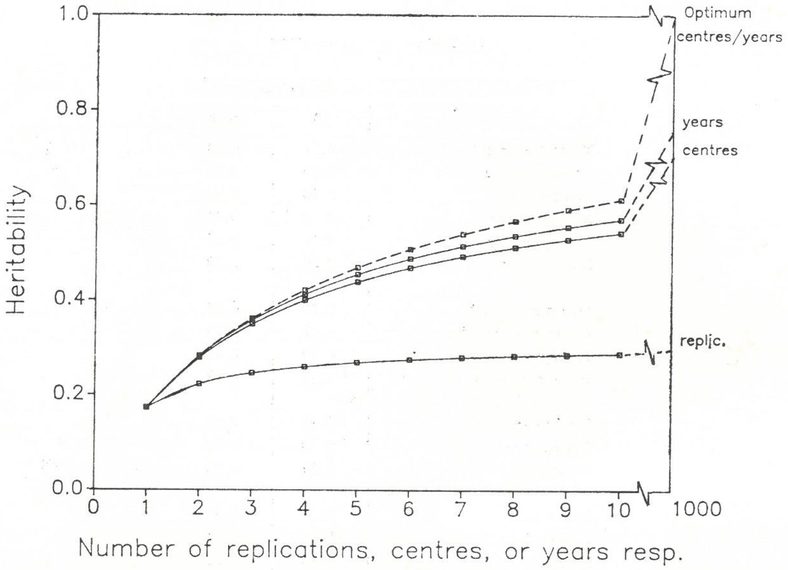

Fig. 3. Heritability as function of number of replications, centres, or years, respectively. Dashed curve for optimal ratio of years and places, for the average variability ratio of cereals

3. The best ratio of number of centres to number of years is given by the ratio of σ_{vc}^2 to σ_{vy}^2 (Schutz, Bernard, 1967). This function is plotted as dashed curve in figure **3**. Heritabilities above 0.8 are only possible in tests both with several centres and several years.

The standard dimensions in the old testing system for cereals in the FRG were 3 years with 12 centres and 6 blocks, i.e. each variety **is** tested on 216 plots. In spite of this large design, table 5 shows rather insufficient heritability values in several crops, e.g. in spring wheat. For recommendation purposes it is desirable to test varieties such that heritabilities above 0.8 are reached (or 0.9 for the square root of heritability, i.e. the correlation between genotype and phenotype of varieties).

5. PRECISION IN UNBALANCED SERIES

If a balanced system of trials is altered in an unbalanced form, as it was the case in cereals, the questions arise, "How high is the precision and which is the 'best' method of estimating variety performance?" In the new variety testing system, the varieties are tested over three years. For each variety, three year means can be calculated:

$\bar{x}_1$ = mean of the first year (from the breeder's trials,
10 centres with 6 replications each)

$\bar{x}_2$ = mean of the second year (from the official trials,
12 centres with 6 replications each)

$\bar{x}_3$ = mean of the third year (from the trials combined with the regional trials of the federal states,
30 centres with 6 replications each).

It is assumed that only two centres are common to the three years. The given numbers of centres per year may be considered as a standard in cereal testing, although the numbers may vary from crop to crop and period to period. The variance ratio of cereals (2) shall be supposed further.

Table 6

Heritability in three different methods of combining season yields

Method	Weights	Heritability
BLUP	0.25 : 0.27 : 0.33	0.845
Mean over years	1 : 1 : 1	0.843
Mean over trials	10 : 12 : 30	0.825

In table 6, three different estimation procedures are compared. For all procedures the heritability (or correlation coefficient) is in the range of heritabilities of column 2 of table 5. Thus the precision of the new system may be acceptably collated to the old. Best linear unbiased prediction (BLUP; see Verdooren, 1987) supplies the optimal weights for the three years and the highest heritability coefficient. The two other procedures using ordinary means show lower precisions. The simple average of the three year means per variety seem to be an efficient and practical method of estimating the performance of the varieties due to simple computation and interpretation. The loss in precision, when compared with BLUP may be negligible.

It should be noted that this simple mean is not the 'best' in all situations. In early generation testing, with small number of centres, the average over the centres means or weighting of the three years by the number of centres (procedure 3) is preferable (Utz 1974). Hill and Rosenberger (1985) compared several procedures ranging from percent of checks to BLUP and found BLUP very attractive in more unbalanced situations than those considered here.

6. DISCUSSION

The derived estimates may be compared with those of two other investigations. Rundfeldt (1970) presented results from the same official trials from earlier years (1962-1965) in cereal crops. He found mostly smaller interaction and plot error variances than given here, which may be in agreement with the lower mean yields in earlier years. In the

United Kingdom, Talbot (1984) published a similar list of estimates for 15 agricultural crops. Some major differences between his study and the present one should be noted. In U.K., varieties × centres variance was smaller in winter wheat, the varieties and the three varieties × environments interactions were smaller in forage maize and field beans, and the varieties × years contribute more than varieties × centres in perennial ryegrass with conservation management. Such differences may be explained by the high estimation errors, as well as by differences in climate, tested population of varieties, or other trial conditions.

Besides the heritability parameters used here, critical differences and the probability of accepting a new variety are discussed in Patterson et al. (1977) and Talbot (1984),

Reliable estimates of components of variance are the necessary basis for optimum allocation of materials, space, and labor in performance tests or to improve efficiency of the selection process. Therefore, it is especially desirable to use the extensive data of variety tests for such enlarged statistical analyses.

Aknowledgement. We are very grateful to Peter Stefany for critical reading of the English text.

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GENETYCZNA I ŚRODOWISKOWA ZMIENNOŚĆ PLONÓW W DOŚWIADCZENIACH OCENY ODMIAN W RFN

Komponenty wariancyjne związane ze zmiennością genetyczną i środowiskową dla 16 gatunków badanych w oficjalnej ocenie odmian w RFN zostały obliczone przy użyciu metody REML. Obliczenia wykonano na podstawie danych doświadczalnych obejmujących od 7 do 11 lat, od kilku do kilkunastu punktów doświadczalnych oraz od kilku do kilkudziesięciu odmian. Wszystkie doświadczenia były przeprowadzone w czterech powtórzeniach w układzie bloków zrandomizowanych kompletnych. We wszystkich gatunkach i seriach doświadczeń największym komponentem wariancyjnym był komponent związany z błędem doświadczalnym. Komponenty wariancyjne dla zbóż ozimych okazały się większe od komponentów dla zbóż jarych. Najmniejsze komponenty dla interakcji genotypowo-środowiskowej otrzymano dla buraka cukrowego. Natomiast kukurydza, trawy i ziemniak charakteryzują się dużymi komponentami wariancyjnymi związanymi zarówno ze zmiennością odmian, jak i zmiennością ich interakcji ze środowiskiem. W pracy porównuje się także obliczone wielkości komponentów wariancyjnych z komponentami otrzymanymi we wcześniejszych badaniach w RFN oraz w Wielkiej Brytanii. Stwierdza się wzrost wielkości komponentów wariancyjnych, co jest najprawdopodobniej związane ze wzrostem poziomu plonowania. Na podstawie wielkości komponentów wariancyjnych dyskutuje się też zagadnienia związane z optymalnym planowaniem nowych serii doświadczeń.

TABELE

Tabela 1. Dane doświadczalne użyte w analizie
Tabela 2. Estymatory komponentów wariancyjnych dla pszenicy ozimej
Tabela 3. Estymatory komponentów wariancyjnych dla wszystkich rozważanych gatunków
Tabela 4. Estymowane współczynniki zmienności komponentów wariancyjnych
Tabela 5. Estymowane współczynniki powtarzalności dla rozważanych gatunków
Tabela 6. Współczynniki powtarzalności dla trzech metod „ważenia" plonów z kolejnych lat

RYSUNKI

Rys. 1. Komponenty wariancyjne zmienności plonu ziarna dla pszenicy i jęczmienia
Rys. 2. Komponenty wariancyjne zmienności plonu ziarna dla zbóż ozimych
Rys. 3. Współczynniki powtarzalności jako funkcja liczby powtórzeń, miejscowości i lat